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Habitat stability and predation pressure affect temperament behaviours in populations of three-spined sticklebacks

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Summary

1. There is growing interest in the causes and consequences of animal temperaments. Temperament behaviours often have heritable components, but ecological variables can also affect them. Numerous variables are likely to differ between habitats, and these may interact to influence temperament behaviours.

2. Temperament behaviours may be correlated within populations (behavioural syndromes), although the underlying causes of such correlations are currently unclear.

3. We analysed three different temperament behaviours and learning ability in three-spined sticklebacks, *Gasterosteus aculeatus*, to determine how different ecological variables influence them both within and between populations. We selected populations from four ponds and four rivers that varied naturally in their exposure to predators.

4. High-predation river populations were significantly less bold than a high-predation pond and low-predation river populations, and low-predation pond populations were significantly less bold than a high-predation pond population. Within populations, temperament behaviours were correlated in one high-predation river population only.

5. These results suggest that multiple ecological factors can interact to affect temperament behaviours between populations, and also correlations in those behaviours within populations.

Key-words: behavioural syndromes, ecology, temperament, three-spined sticklebacks (*Gasterosteus aculeatus*).

Introduction

Intraspecific differences in temperament behaviours were considered traditionally non-adaptive variations surrounding an adaptive optimum. It has taken some time for researchers to accept that animals, like humans, display distinct character or temperament traits (sometimes referred to as 'personality traits' or 'personality behaviours'). Here, we use 'temperament' to describe an animal's responses to particular situations, e.g. willingness to take or avoid risks. Recently it has been suggested that variations in temperament may, in fact, be adaptive (e.g. Wilson 1998; Dall, Houston & McNamara 2004). It has been proposed that animals exhibit temperament behaviours that are similar to the five axes of personality used by psychologists to describe human behaviour (the human five-factor model: see Gosling & John 1999). Borrowing from these ideas, research has begun to address whether animals express similar types of temperament (see Gosling 2001 for a review). This has revealed that temperament behaviours generally have a heritable component (e.g. Bouchard & Loehlin 2001; Dingemanse *et al.* 2002).

The environment experienced during development can also shape temperament behaviours, e.g. in captive reared species of fish (Huntingford & Adams 2005). Enhancing the spatial complexity of the rearing environment alters behaviour towards prey, exploratory and stress recovery behaviours in hatchery-reared cod, *Gadus morhua* (Braithwaite & Salvanes 2005). Similarly, hatchery-reared brown trout, *Salmo trutta*, are bolder than wild trout (Sundstrom *et al.* 2004). Less attention has been directed at how the natural environmental might shape temperament. A recent study investigated boldness in natural populations of the tropical poecillid, *Brachyraphis episcopi*, and found that fish originating from high-predation areas were bolder than those from low-predation sites (Brown, Jones & Braithwaite 2005).

Alongside differences between populations, different temperament behaviours (e.g. aggression and boldness) or the same temperament behaviour in different functional contexts (e.g. boldness towards a predator and boldness towards a

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competitor) can be correlated within populations, and this is known as a behavioural syndrome (e.g. Gosling 2001; see Sih *et al*. 2004; Sih, Bell & Johnson 2004 and Bell 2007 for reviews on behavioural syndromes). For instance, correlations between anti-predator behaviours and activity levels have been found in chaffinches (Quinn & Cresswell 2005). There are two hypotheses for the existence of behavioural syndromes. The 'constraints' hypothesis states that when correlations exist between behaviours it is because of underlying constraints that are difficult to break apart and so necessarily couple behaviours together. For example, behaviours may be either linked proximally or due to the pleiotropic effects of genes, so that selection on one behaviour causes correlated changes in another (Bell 2005). This hypothesis has been used to explain why some behaviours may appear maladaptive when considered in one functional context only. For example, populations of the desert spider *Agelenopsis aperta* living in food-limited environments are more likely to attack and also to kill more prey than they can consume, and this apparently energetically wasteful behaviour is presumed to be a consequence of selection for general aggressiveness towards prey in food-limited environments (Maupin & Riechert 2001). The second hypothesis, the 'adaptive' hypothesis, proposes that when correlations between behaviours exist it is because they are adaptive (Wilson 1998; Bell 2005). In the spider example given above, this hypothesis suggests that spiders living in food-limited environments show a greater tendency to attack prey and participate in superfluous killing because both behaviours are beneficial in this environment. At present, it is difficult to imagine how superfluous killing could be adaptive in this system (Maupin & Riechert 2001). A way to disentangle these two hypotheses is to investigate the presence/absence of behavioural syndromes within populations of the same species. If the 'constraints' hypothesis is true, when certain behaviours are correlated within one population, then due to underlying constraints they must necessarily be correlated within all others. A recent study on two populations of three-spined sticklebacks revealed that this was not the case for this species, as there were genetic and phenotypic correlations of activity, aggression and boldness in one population only (Bell 2005). The reasons why these behaviours were correlated within one population but not the other are unclear, although differences in predation pressure were suggested.

Typically, studies of behaviour consider the effects of only one ecological variable at a time. This may be misleading, as numerous ecological variables are likely to differ between habitats, and may interact to influence behavioural phenotypes. To date, no study has investigated the effects of multiple ecological variables on temperament, or how these variables may interact. Hence, we designed an experiment to investigate how two natural variables affect temperament and learning behaviours. Using three-spined sticklebacks (hereafter, sticklebacks) from ponds (stable habitat) and rivers (unstable habitat) that varied naturally in predation pressure, we quantified three temperament behaviours: boldness, neophobia and activity in an unfamiliar environment in the presence of a novel object. We also investigated learning rate in a simple foraging task. Between populations, we predicted that high-predation-site fish would be less bold, more neophobic and have lower activity levels in order to decrease the chances of being detected by a predator. Animals experiencing higher levels of predation often display enhanced anti-predator behaviour and morphology [e.g. sticklebacks (Giles & Huntingford 1984; Bell 2005), guppies, *Poecilia reticulata* (Seghers 1974; O'Steen, Cullum & Bennett 2002), Daphnia spp. (Fisk *et al*. 2007), larval anuran spp. (Relyea 2001) and Seychelles warblers, *Acrocephalus sechellensis* (Veen *et al*. 2000)]. We also predicted that activity and neophobia would be correlated, because they were measured closer together in time than the other behaviours.

Learning rate could be affected in two ways by temperament: (1) bolder, less neophobic, more active fish may learn a spatial foraging task faster because they explore their environment and have a higher chance of encountering food items. This appears to be the case with guppies and trout, where bolder individuals learn foraging tasks faster (Dugatkin & Alfieri 2003; Sneddon 2003). (2) Less bold, less active and more neophobic individuals may learn faster if they are more careful and pay greater attention to their environment, as found in great tits *Parus major* (e.g. Marchetti & Drent 2000; see Korte *et al*. 2005 for a review). We had no specific hypothesis for how habitat stability might affect temperament, but because it has been found previously to affect learning in sticklebacks (Girvan & Braithwaite 1998; Braithwaite & Girvan 2003), we considered it might also have an effect on behaviours associated with temperament.

Methods

SUBJECTS AND HOUSING

Minnow traps and large nets were used to collect sticklebacks in November 2004 and 2005 from four ponds and four rivers in central and southern Scotland, UK. The ponds were: Beecraig Pond (3°47′ W, 55°57′ N), Craiglockhart Pond (3°14′ W, 55°55′ N), North Belton Pond (2°35′ W, 55°59′ N) and Balmaha Pond (4°31·5′ W, 56°05′ N); the rivers were: Water of Leith (3°14′ W, 55°57′ N), River Biel (2°35′ W, 55°59′ N), River Endrick (4°24′ W, 56°02′ N) and River Esk (3°10′ W, 55°51′ N). Sixty-six fish were tested (10 from River Biel and eight from all other sites). Populations were housed separately in holding tanks (76 cm long × 30 cm wide × 38 cm high) furnished with plastic plants, a gravel substrate, biofilters and refuges. Fish were fed on bloodworm. Laboratory temperature was maintained on a day : night cycle at 14 : 9·5 °C, and a light : dark cycle of 10 : 14 h. Fish were collected outside their breeding season, and as males and females are identical morphologically at this time and school together, populations were assumed to be mixed-sex. All populations were of a similar mean body length [analysis of variance (ANOVA): $F_{7,57} = 1{\cdot}4$, $P = 0{\cdot}2$, mean = 3·7 cm ± 4·6 standard deviation (SD)].

QUANTIFYING PREDATION PRESSURE

Using a combination of direct field measurements and fish body armour, we classified fish as coming from either high- or low-predation sites (Table 1). Details of the analyses and methods used to assign populations to high- or low-predation categories are given in Brydges *et al*. 2007).

Table 1. Categorization of field sites as either high or low predation. Predation pressure was determined using morphological measurements of the defensive armour of fish (following methods employed in Vamosi & Schluter 2004), and electrofishing for piscivorous predators at each of the sites

Site	Predation category
Beecraig Pond	Low
Craiglockhart Pond	High
North Belton Pond	Low
Balmaha Pond	Low
Water of Leith	High
River Biel	High
River Endrick	Low
River Esk	Low

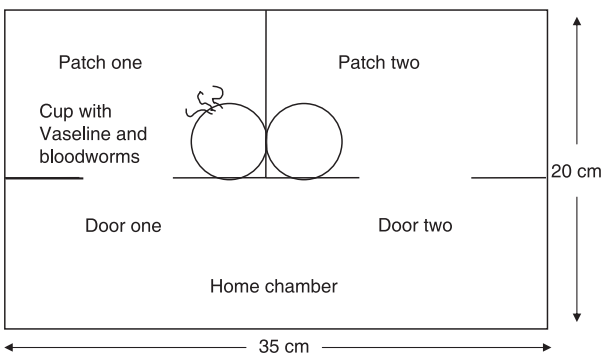

Fig. 1. Schematic view of a tank used to house fish individually during boldness assay 1.

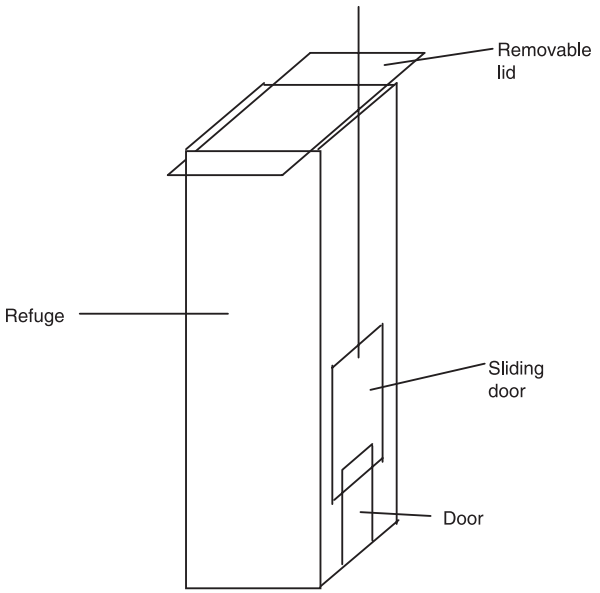

Fig. 2. Diagram of boldness box apparatus used to assay the second measure of boldness.

QUANTIFYING TEMPERAMENT BEHAVIOURS

Boldness assay 1

Boldness was quantified using two methods. The first was derived from an earlier study (Brydges *et al*. 2007) and involved determining the average time taken for a fish to begin a foraging trial. We chose this as our first measure of boldness because we expected that all fish would be highly motivated to forage, as they were maintained on a small diet of three bloodworms a day during the experiment, so the only factor preventing them from foraging should be their willingness to swim across the home chamber and enter a foraging compartment. Fish were housed individually in tanks (35 cm long × 20 cm wide × 24·5 cm) with a water depth of 15 cm, 1 cm of gravel substrate and an individual biofilter. To allow fish visual access to one another and reduce isolation stress in this naturally shoaling species, tanks were placed next to one another in a row. These tanks were divided into three sections, a home chamber and two foraging patches using plastic dividers (Fig. 1). A small, weighted plastic food cup was placed into each of the foraging compartments. Fish were trained to find food (bloodworms) in one of the two compartments, and were given two trials a day. During a trial, plastic dividers were placed down the sides of the tank to prevent fish from watching and learning the task from neighbours. Food was placed into one of the food cups, and latency to enter a compartment was recorded. Fish were trained in this way until they entered the baited patch first in nine of 10 trials (phase 1). When fish had attained this criterion, they were trained with food in the opposite compartment, again until they had entered the baited patch first in nine of 10 trials (phase 2). Half the fish from each population were trained on the left side in phase 1 then the right side in phase 2, and vice versa for the remaining fish. Average latency over the first 10 trials of phases 1 and 2 comprised the first boldness score, with fish that entered a compartment sooner being defined as bolder.

Boldness assay 2

One week after the end of boldness assay 1, fish participated in boldness assay 2. This was based on the method used by Brown *et al*. (2005), and involved timing fish to emerge from a darkened, enclosed box (refuge). We considered this to be a suitable measure of boldness, as fish had to emerge from this dark box into a brightly lit, novel tank environment. Fish were netted individually from their holding tanks and placed into a rectangular test tank (44·5 cm long × 24·5 cm wide × 21·5 cm high) covered with black plastic to reduce outside disturbances. The fish were put into a darkened, enclosed box (refuge) (10·5 cm long × 11 cm wide × 21·5 cm high) with a removable lid that was located in the test tank. This box had a door cut into it (6 cm wide × 9 cm high) that was closed with a sliding door (10 cm wide × 24 cm high). The box was positioned at one end of the rectangular tank on a white plastic semicircle (see Fig. 2). Fish were left to settle for 2 min before the door was raised remotely via a length of monofilament, and to reduce disturbance to the fish all observations were made via a video camera positioned above the tank. Time taken for the fish to emerge fully from the box was recorded. Fish were given a maximum of 15 min to emerge, after which time they were assigned a maximum score of 900 s. Fish that emerged sooner were assumed to be bolder.

Neophobia

The day after boldness assay 2, neophobia was quantified using two methods. Fish were netted individually from their home tanks into

a test tank (44·5 cm long, 24·5 cm wide, 21·5 cm high) containing a novel object (this was a brightly coloured red and blue plastic toy, measuring 6 cm long × 6 cm wide × 1 cm high). Animals generally find novel objects aversive, and this object was novel for all fish, so we considered this an appropriate measure of neophobia. The test tank was marked on the outside to create three equal-sized sections, and the novel object was placed in the left section for half of each population of fish, the right section for the others. Fish were placed initially into a clear plastic cylinder (diameter 5 cm, height 8 cm) in the middle section of the tank to standardize start location. They were given 2 min to settle, then the cylinder was gently raised remotely via a fine monofilament. Observations were made via a video camera, filming from above, and the tank was covered in black plastic to minimize external disturbances to the fish. Trials were filmed for 15 min. Video replay was used to determine the time fish spent in the near, middle and far sections of the tank relative to the novel object. Fish that spent a larger proportion of time near the novel object were considered to be less neophobic, and this was the first measure of neophobia. Time taken for fish to approach the novel object was also recorded as a second measure.

Activity in a novel environment

Activity in a novel environment was determined during the neophobia trial. This tank was a novel environment for all fish. Over the 15 min, the number of times a fish crossed between the near, middle and far sections was recorded to give an 'activity' score for each fish.

Learning rate

The average number of trials taken for a fish to learn the foraging task presented in phases 1 and 2 of boldness assay 1 was determined.

ANALYSIS

One fish from North Belton was excluded from the analysis as it did not complete successfully the learning task presented in boldness assay 1. Temperament was measured in three different contexts: boldness, neophobia and activity. There was one measure for activity, but two measures each for boldness and neophobia. In order to obtain single measures of boldness and neophobia, principal components analyses (PCA) were run on the behaviours in each context. By reducing the dimensions of each characteristic from two to one the analysis was simplified, thus reducing the problem of multiple comparisons. For boldness, PC1 accounted for 74% of the variation in the data, with loading coefficients of 0·71 for average time to begin a foraging trial (boldness assay 1) and 0·71 for time to emerge from a box (boldness assay 2). The more positive the value, the longer a fish took to emerge from the box and begin the foraging trial (i.e. less bold fish). For neophobia, PC1 accounted for 73% of the variation in the data, with loading coefficients of –0·7 for time to approach the novel object and 0·7 for time spent near the novel object. The more positive the value, the longer a fish took to approach the novel object and the less time it spent near it (i.e. more neophobic fish).

To investigate the effects of temperament behaviours between populations, separate ANOVAs were run with activity, PC1 of boldness and PC1 of neophobia as dependent variables using fish length, replicate, population (a random factor nested within predation pressure and habitat type), habitat type, predation pressure and habitat type × predation pressure in the models. Non-significant terms were removed in a stepwise fashion to leave minimal models.

We used general linear models to investigate the relationship between temperament behaviours within populations. Here, the four dependent variables were the number of trials taken to learn the task in boldness assay 1, activity, PC1 boldness and PC1 neophobia, and these investigated the effects of fish length, replicate, population, number of trials to learn the task presented in boldness assay 1, activity, PC1 boldness and PC1 neophobia (with the dependent variable affecting which of these factors were included in each analysis). Non-significant terms were removed in a stepwise fashion to leave minimal models.

Results

EFFECTS OF TEMPERAMENT BETWEEN POPULATIONS

There was a significant main effect of population ($F_{4,57} = 19$, $P < 0{\cdot}001$) and a significant predation × habitat interaction ($F_{1,57} = 19$, $P < 0{\cdot}001$), but no overall effects of predation ($F_{1,57} = 0{\cdot}028$, $P = 0{\cdot}86$) or habitat ($F_{1,57} = 1{\cdot}43$, $P = 0{\cdot}24$) on boldness. A *post-hoc* Tukey test revealed that the predation pressure × habitat interaction arose because low-predation river fish and high-predation pond fish were significantly more bold than high-predation river fish, whereas low-predation pond fish were more timid than high-predation pond fish (Fig. 3a). A *post-hoc* Tukey test on population revealed a similar pattern to the predation pressure × habitat interaction, with low-predation river fish and high-predation pond fish being more bold than high-predation river fish, and low-predation pond fish more timid than high-predation pond fish.

There were no overall effects of predation ($F_{1,57} = 0{\cdot}90$, $P = 0{\cdot}35$) or habitat ($F_{1,57} = 0{\cdot}04$, $P = 0{\cdot}83$) on activity in a novel environment, but there was a significant predation × habitat interaction ($F_{1,57} = 6{\cdot}27$, $P = 0{\cdot}02$). There was also a significant effect of population ($F_{1,57} = 4{\cdot}89$, $P = 0{\cdot}002$). A *post-hoc* Tukey test on the predation pressure × habitat interaction revealed that although predation pressure appears to affect activity in different ways in river and pond habitats, none of the means of the groups were significantly different to one another (Fig. 3b). A *post-hoc* Tukey test on population revealed that River Biel fish were significantly less active than Water of Leith and Craiglockhart Pond fish. There were no significant effects on neophobia ($F_{11,53} = 15{\cdot}86$, $P = 0{\cdot}13$) (Fig. 3c).

EFFECTS OF TEMPERAMENT WITHIN POPULATIONS

The relationship between boldness and activity differed among the populations (population × activity interaction $F_{7,49} = 3{\cdot}28$, $P = 0{\cdot}006$), with a negative relationship between boldness and activity in the River Biel population ($t = -4{\cdot}17$, $P = 0{\cdot}0001$; Fig. 4), but not in any other populations. Boldness and activity were not related to any other measures within populations. Similarly, there was no relationship between either neophobia ($F_{38,26} = 0{\cdot}72$, $P = 0{\cdot}82$) or the number of trials taken to learn the task in boldness assay 1 ($F_{38,26} = 2{\cdot}56$, $P = 0{\cdot}7$) and any of the other measures.

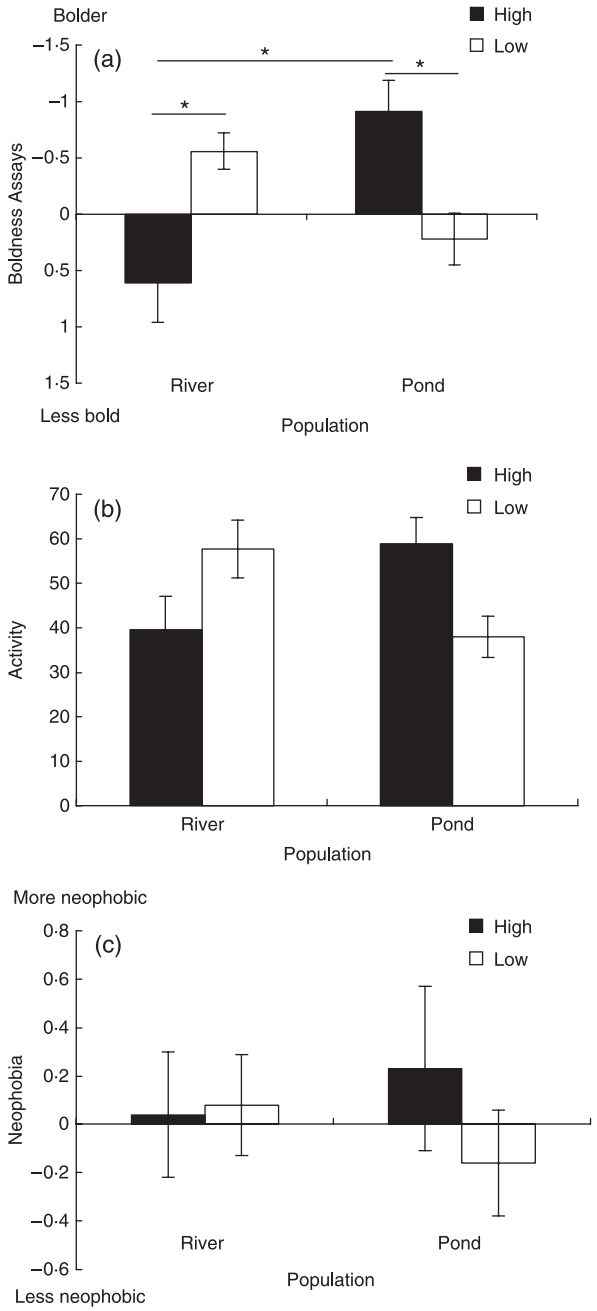

Fig. 3. (a) Principal component score of boldness behaviours for pond and river fish from habitats of differing predation pressure. Bars connected by an asterisk are significantly different to one another. Error bars represent one standard error. (b) Activity scores for pond and river fish from habitats of differing predation pressure. Error bars represent one standard error. (c) Principal component score of neophobia behaviours for pond and river fish from habitats of differing predation pressure. Error bars represent one standard error.

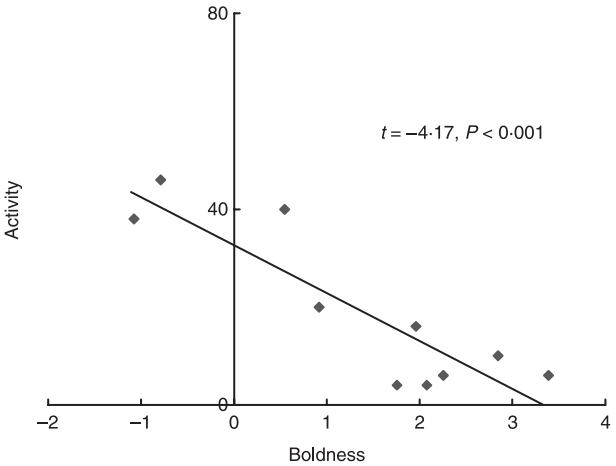

Fig. 4. Correlation between activity and PCI boldness for River Biel fish.

Discussion

High-predation river fish were less bold and tended to be less active than high-predation pond fish and low-predation river fish. Although difficult to determine precisely what factors drive these differences, the results suggest that predation pressure and habitat stability can potentially interact to influence temperament in sticklebacks. As only one high-predation pond was sampled, it is difficult to conclude that differences in spatial habitat stability, rather than a unique feature of Craiglockhart Pond, are driving this difference; however, habitat stability has been found previously to alter behaviour in sticklebacks (Girvan & Braithwaite 1998; Braithwaite & Girvan 2003).

In agreement with our original hypothesis, low-predation river fish were bolder and tended to be more active than high-predation river fish. Similarly, Bell (2005) found that a low-predation river population of sticklebacks was more active than a high-predation population. Predators have long been known to influence the behaviour of their prey. Fish sampled from high-predation sites often display greater anti-predator behaviours (e.g. three-spined sticklebacks: Giles & Huntingford 1984; guppies: Seghers 1974) than those from low-predation sites. Indeed, longer emergence times and lower activity levels will decrease the chances of meeting a predator in a high-predation environment.

Temperament behaviours of boldness and activity were correlated in River Biel fish only, with bolder fish having higher activity levels. Some caution should accompany this result, as only 10 individuals were used from this population, however, the correlation was highly significant, and different to the relationship between boldness and activity in the other populations. There were no such correlations for any other populations. Similarly, a recent study found genetic and phenotypic correlations of activity, aggressiveness and boldness in a high- but not a low-predation population of river sticklebacks (Bell 2005). This suggests that the high-predation river environment may be selecting for these two behaviours to become correlated. Further evidence that predation pressure influences correlations between temperament behaviours comes from two recent studies. A population of sticklebacks originating from a low-predation environment initially displayed no correlation between boldness and aggression, but exposure to a trout induced a correlation (Bell & Sih 2007).

Similarly, aggressiveness, activity and novelty reactions were correlated more tightly in pond populations of sticklebacks living with predators compared to those living without (Dingemanse *et al*. 2007). However, in the present study no correlation was unveiled in one other high-predation river population, the River Endrick. This may be due to slightly lower levels of predation in this habitat compared to the River Biel [which was the highest predation habitat (Brydges *et al*. in press)]. However, it may also be due to other factors more specific to the River Biel site. It would be interesting to investigate correlations in other river habitats with predation pressure comparable to that of the River Biel.

The 'constraints' hypothesis for the existence of behavioural syndromes predicts that if temperament behaviours are correlated within one population, then owing to underlying constraints they must necessarily be correlated in all other populations of that species. In conjunction with the results presented by Bell (2005), this study does not support that conclusion. This suggests that when correlations do exist between behaviours it is because they are beneficial, rather than due to underlying constraints.

We also predicted that there may be a correlation between temperament behaviours and learning rate. Within populations, however, there were no correlations between temperament behaviours and learning rate in boldness assay 1, suggesting that in contrast to other species [e.g. trout (Sneddon 2003), guppies (Dugatkin & Alfieri 2003) and great tits (Marchetti & Drent 2000)], boldness, neophobia and activity do not impact upon learning in sticklebacks. However, the nature of the learning task presented and methods used to quantify temperament behaviours need to be taken into account. There are many potential ways to define boldness, e.g. boldness in the face of a predator vs. time taken to emerge from a refuge. There are also numerous ways to measure it. In the present study, we defined boldness as time taken to emerge from a refuge. In previous studies, where correlations were found between boldness and learning, boldness was measured as a method used to capture food (Sneddon 2003), and predator inspection behaviour (Dugatkin & Alfieri 2003). Furthermore, the task presented differs from that in the present study, and simply involved fish learning to associate food with a food ring placed on the water. Bold fish that are not afraid of approaching a novel food ring may have a distinct advantage in learning such a task. In contrast, in the present study fish had the more complicated task of encoding spatial location in order to find food patches, and here boldness may not have such an impact on learning rate. Thus the nature of the learning experiment and methods used to quantify temperament behaviours need to be considered when interpreting results of such studies.

Several studies (reviewed in Sih *et al*. 2004) have found correlations between temperaments at the population level. For example, more exploratory parrot species either lived in low-predation habitats, fed on complex foods or lived in complex habitats (Mettke-Hoffman, Winkler & Leisler 2002). These associations were proposed to occur because it was either more beneficial or less costly to explore certain environments. Similarly in the present study, low-predation river fish were not only bolder than high-predation river fish, but have been found previously to learn faster (Brydges *et al*. in press). Here, it may be less costly for low-predation river fish to be bolder, allowing them to learn faster.

In conclusion, our results suggest that ecological variables can play a substantial role in shaping temperament behaviours between populations, and that multiple variables may interact when fine-tuning behaviour. Although the underlying reasons are currently unclear, we have shown that certain temperament behaviours are correlated within some populations but not others, providing further evidence for the 'adaptation' hypothesis for the existence of behavioural syndromes. Our results demonstrate the importance of considering multiple ecological variables when investigating the role of the environment in shaping behaviour.

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